

**PREY SELECTION AND DIURNAL ACTIVITY OF
HOLCOCEPHALA OCLATA (F.) (DIPTERA: ASILIDAE) IN
COSTA RICA**

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Abstract.—*Holcocephala oculata* (F.) is an abundant small robber fly in open areas at La Selva Biological Station, Costa Rica, and was studied during August 1995. The majority (92%) of prey taken by *H. oculata* belong to the orders Hymenoptera, Diptera, and Coleoptera, with the remaining belonging, in order of decreasing frequency, to Hemiptera, Thysanoptera, Homoptera, Araneida, Strepsiptera, and Psocoptera. A comparison of sticky trap samples of flying insects and robber fly prey items reveal differences in the proportion of orders represented. Either *H. oculata* prefers particular orders of prey, or sticky traps are inadequate in sampling insect faunas. Cannibalism was not observed for *H. oculata*. Flies are more numerous in sunny areas at the beginning and end of the day. Flies are rarely observed in exposed areas on clear days when incident radiation is high. Areas shaded from direct incident radiation through the day show little change in fly numbers. Courtship and copulation, described herein, generally occur after 1200. *Holcocephala oculata* perches less than a meter off the ground, on average, with grass species tending to be the substrate most often chosen. No evidence for invertebrate predation on *H. oculata* was found, although several suitable predaceous arthropods co-occur with the robber fly and at least one, the ponerine ant *Ectatomma ruidum* Roger, readily attacked robber flies during feeding trials.

Key Words: Asilidae, *Holcocephala oculata*, robber fly, prey selection, courtship, diurnal activity, La Selva Biological Station, Costa Rica

Robber flies are among the larger and more visible members of the Diptera but are poorly understood when it comes to details of their ecology and behavior. A number of temperate zone Asilidae have been studied in detail (Lavigne and Holland 1969; Hespeneide and Rubke 1977; Hespeneide 1978, 1989; Weeks and Hespeneide 1985), but only a few tropical species (Fisher 1983; Shelly 1984a, 1988; Fisher and Hespeneide 1992). These flies typically capture their prey by waiting at a perch, intercepting the prey in mid-flight, and then returning to the perch and consuming the

item externally. In addition, some members of this group have courtship displays that usually involve characteristic aerial maneuvers on the part of the male (Fisher and Hespeneide 1982, 1992).

Holcocephala oculata (F.) (Dasypogoniinae: Danilini; Fig. 1) is the smallest (mean length 5.20 mm; $n = 10$) of four species of *Holcocephala* that are known to occur at La Selva Biological Station, Costa Rica (E. Fisher and H. A. Hespeneide, unpublished). Adults perch on low-growing vegetation in open areas. Here I describe the prey selection and diurnal activity of *H.*



Fig. 1. *Holcocephala oculata* showing typical perch behavior.

oculata and test the hypothesis that net incident radiation affects robber fly densities more than ambient temperature or time of day.

MATERIALS AND METHODS

The data were collected during 10 separate days between 9–29 August 1995 at the Organization for Tropical Studies' La Selva Biological Station which is located at the confluence of the Río Puerto Viejo and Río Sarapiquí, Heredia Province, Costa Rica (McDade et al. 1994).

I chose two 50 m transects along weedy margins bordering mono- and polyculture plots within the "Huertos" project, an ongoing study on the sustainability of soil fertility in reconstructed tropical ecosystems (J. Ewel, personal communication). One transect was continually exposed to the sun from dawn until dusk ("sunny") whereas the other was shaded most of the time

("shady"). In addition to the transects, neighboring weedy margins within the Huertos project were used for additional behavioral and ecological observations on *H. oculata*. The weedy margins are cut at three to six month intervals and maintained at a height of less than three meters, and include several species of grasses, the most common being *Paspalum conjugatum* Berg., *Digitaria* sp., and *Cynodon dactylon* (L.) Pers. In addition, sedges (*Cyperus* spp.), and a diverse assemblage of plant species adapted to disturbed areas are common within the margins, as are fallen stems and leaves from adjacent tree plots.

At least five additional asilid species (three *Holcocephala*, one *Atractia*, one *Mallophora*) also co-occur with *H. oculata* in the weedy margins, and many species of predaceous arthropods may be found there as well (personal observation). The biology of one other species (*H. affinis* (Bellardi)) has been studied at La Selva and is generally similar to that of *H. oculata* (H. A. Hespenheide, unpublished).

To determine the diversity of prey taken by *H. oculata*, I captured feeding robber flies in the sunny transect during the 10 days and collected their prey items. Prey were collected by placing a plastic vial over a robber fly disturbing it so that it released the prey item into the vial, after which the robber fly was released. Preliminary captures revealed no detrimental effects due to this method of removing prey from the robber flies; released individuals remained in the transect and were often seen with a new prey item moments later. This method of prey removal has been used by others (see Hespenheide and Rubke 1977; Hespenheide 1978, 1989; Shelley 1984a, 1988). I recorded the time at which the prey item was collected in order to observe any temporal pattern in prey choice. Prey were not sampled from robber flies in the shady transect.

To gather information on the diversity of available prey items, I placed two sticky traps (21.5 × 28 cm transparencies coated with Tanglefoot®) on poles 1 m above the

ground in the sunny transect during study days 8–10 while the robber flies were being sampled. Only arthropods measuring up to 4.3 mm (the maximum prey size collected from *H. oculata*) were considered in the analysis of the sticky traps. I identified prey and sticky trap samples to order. To determine if *H. oculata* exhibits a preference for certain prey over others or is behaving opportunistically, I performed two analyses to compare the actual robber fly prey with the available prey gathered from sticky traps. In one analysis I compared a subsample of the actual prey collected during the days the sticky trap samples were being employed (days 8–10). In a second analysis I included the entire actual prey sample collected during the 10 sampling days.

To determine the daily cycle of *H. oculata*, I censused flies on all 10 days dividing each into five two-hour periods beginning at 0800 h and ending at 1600 h. I conducted a census at the beginning of each of the five periods. Flies in the shady transect were simply counted while those in the sunny transect were counted and assigned to one of four activities: Feeding, copulating, courting, or other. The activity “other” included flies that were perched but not feeding and those that were flying between perches. During the intervening time periods, I kept out of the transects to minimize my disturbing the flies.

Prior observations on the daily cycle of *H. oculata* indicated that individuals avoided areas exposed to direct sunlight during the hottest times of the day, especially on clear days. I gathered data on ambient temperature and incident radiation to determine possible influences on the daily cycle of *H. oculata*. My hypothesis was that net radiation was more important than temperature or time of day in determining robber fly density in a given area; the null hypothesis was that there was no difference among the three independent variables in determining robber fly density. Net radiation was measured with a net radiometer monitored by the Huertos project. Ambient temperature

was measured at a single fixed location in the shade between the two transects.

To describe the courtship behavior of *H. oculata*, I surveyed the transects during the study periods and observed courting pairs. I recorded the time and noted whether the outcome of the courting attempt was successful or unsuccessful in initiating copulation.

To determine whether or not *H. oculata* exhibits a preference for type or height of perch, I walked the weedy margins in and around the transects and recorded the choice of perch substrate, location on substrate, and height of perch above ground for all *H. oculata* encountered. The location was defined as precisely where on the substrate the fly chose to perch. Above ground height referred to the shortest distance between the fly's position on the substrate and the ground.

For all analyses, data on mean values are evaluated with the non-parametric Wilcoxon sign rank test, and contingency tables employing the *G*-test or Fisher's exact test are used to compare percentile data.

The arthropod predators most often observed in the transects foraging on substrates used by *H. oculata* were *Ectatomma ruidum* Roger, an aggressive ponerine ant, and orb-weaving spiders (Araneidae). I performed feeding trials to determine the palatability of this fly to *E. ruidum* with robber flies disabled by having one wing removed. Orb-weavers construct webs in the weedy margins at the level of *H. oculata*'s perch heights. Because prey items accumulate in these webs, information on the spider's prey choice is readily available. I carefully removed the silk from entrapped prey to establish whether *H. oculata* was among those preyed upon by the spiders. Other arthropod predators observed included jumping spiders (Salticidae), which have been observed to take robber flies (H. A. Hespenheide personal communication), and tiger beetles (Cicindelidae). However, I observed so few individuals ($n = 4$ and $n =$

2, respectively) that I am unable to evaluate their potential as robber fly predators.

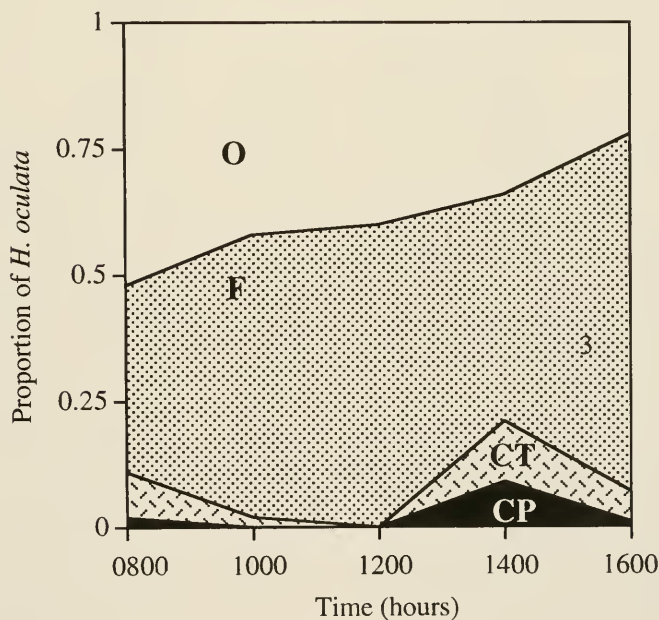
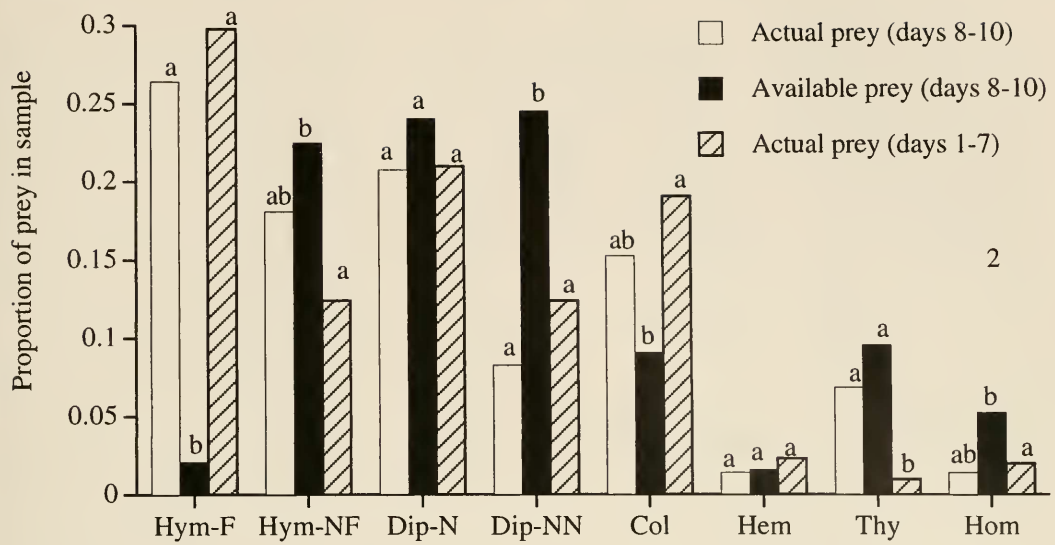
RESULTS AND DISCUSSION

I collected nine orders of arthropod prey from *H. oculata* (Table 1). Among these the Hymenoptera, Diptera, and Coleoptera together account for 92% of the total prey sample. The most frequent prey at the study site were ant reproductives (28.5%). The average prey size was 1.48 mm ($n = 379$) with a range of 0.4 mm (nematocerous Diptera) to 4.3 mm (Coleoptera). Hymenoptera, Diptera, and Coleoptera were also found to dominate prey samples of *Holcocephala fusca* Bromley and *H. abdominalis* (Say) in the eastern United States (Dennis 1979, Scarbrough 1982). However, *H. calva* (Loew), also from the eastern United States and while showing a similar preference for Hymenoptera and Diptera, differs from other *Holcocephala* studied to date by preferring Hemiptera, Homoptera, and Psocoptera over Coleoptera (Scarbrough 1982). The predator to prey size ratio for *H. oculata* is 3.51 (mean robber fly length 5.20 mm). This is identical to that determined for *H. fusca* (3.5, mean robber fly length 5.9 mm; Dennis 1979), and intermediate between *H. abdominalis* and *H. calva* (3.4 and 3.7, respectively, mean robber fly lengths 5.81 mm and 7.25 mm, respectively; Scarbrough 1982). Compared to other asilid genera, the predator to prey size ratio for *H. oculata* is close to that reported for the similarly sized robber fly *Nannocyrtopogon neoculatus* Wilcox and Martin (3.66, mean robber fly length 6.62 mm) in the southwestern United States (Hespenheide 1978), but differs from that reported for the much larger *Stichopogon trifasciatus* (Say) (2.23, mean robber fly length 13.00 mm), also from the southwestern United States (Weeks and Hespenheide 1985). No incidence of cannibalism by *H. oculata* was observed.

Factors that contribute to prey choice for particular asilid species likely include the relative difficulty in handling prey as well as the availability of prey in space and time

(Lavigne and Holland 1969, Hespenheide and Rubke 1977). For *H. oculata*, comparisons of available prey from sticky traps with actual prey collected during the same period (days 8–10) and actual prey from the remaining days (days 1–7) show dissimilar proportions with respect to some prey orders (Fig. 2). For days 8–10, Hymenoptera, Diptera, and Coleoptera are the predominant orders of actual prey of *H. oculata* as well as of sticky trap samples at 90% and 83%, respectively. In general, there is no significant difference between the two subsamples of actual prey. This could indicate that *H. oculata* is consistent in prey choice, or that the relative availability of prey changed little over the course of the study. The higher proportion of formicid Hymenoptera among prey could be the result of robber flies preferring this group. The higher proportion of non-nematocerous Diptera in the sticky trap samples could be due to robber flies not favoring this group, perhaps because they are generally too difficult to capture. These results are in contrast to those found by Shelly (1984a) for *Atractia marginata* Osten Sacken in Panamá where non-nematocerous Diptera composed a lower proportion of prey relative to what was available from sticky traps, and Hymenoptera were insufficiently represented in either sample. Alternatively, the differences observed between robber fly prey and sticky trap samples may be an artifact of the limited ability of sticky traps to adequately sample them, and of sticky traps themselves being more attractive to some taxa than others (Shelly 1984b, 1988; Mensah 1996).

Size comparisons among and between actual and available prey also reveal significant differences (Table 1). In general, there is no difference ($P > .8$; Wilcoxon rank sum test) between the average size prey taken by *H. oculata* and the average size prey available to it. Differences emerge, however, when comparisons are made between individual prey orders. These results indicate that *H. oculata* prefers significantly



Figs. 2–3. 2, Proportions of actual and potential prey of *H. oculata*: available prey from sticky traps (days 8–10; closed bars), actual prey from *H. oculata* (days 8–10; open bars), and remaining actual prey (days 1–7; cross-hatched bars). Relationships among taxa that are significantly different at $P < .05$ (G -test) are represented by different letters. Prey taxa are defined as follows: Hym-F ants; Hym-NF, non-ant Hymenoptera; Dip-N, nematocerous Diptera; Dip-NN, non-nematocerous Diptera; Col, Coleoptera; Hem, Hemiptera; Thy, Thysanoptera; Hom, Homoptera. 3, Proportion of *H. oculata* involved in various activities at each census period. Values for each census period are summed over the 10 study days. CP = copulating, CT = courting, F = feeding, O = other (i.e., perched without prey or flying).

Table 1. Characteristics of actual prey taken by *H. oculata* and available prey collected on sticky traps at La Selva Biological Station Costa Rica. Data on the number collected (No.), percent of sample, and size are presented for the orders represented in the samples. Analyses of size comparisons A and B are explained in the footnotes.

Order ^a	Actual Prey from <i>H. oculata</i>					Actual Prey from Sticky Traps				
	No.	%	Size (mm)			No.	%	Size (mm)		
			Mean	SE ^a	Range			Mean	SE ^a	Range
Hym-F	108	28.5	2.50	.06	1.2-4.2	4	2.2	2.28	.18	2.1-2.8
Hym-NF	50	13.2	1.10	.06	0.5-2.2	42	22.7	0.88	.08	0.4-3.5
Dip-N	78	20.6	1.00	.06	0.4-4.0	45	24.3	1.22	.07	0.6-3.5
Dip-NN	43	11.3	1.10	.05	0.5-2.0	46	24.9	1.45	.11	0.7-4.1
Col	68	17.9	1.80	.10	0.5-4.3	17	9.2	3.12	.17	1.0-4.0
Hem	8	2.1	1.80	.16	1.2-2.3	3	1.6	1.67	.03	1.6-1.7
Thy	8	2.1	1.30	.17	0.8-2.2	18	9.7	1.16	.06	0.9-1.7
Hom	7	1.9	2.40	.20	2.0-3.5	10	5.4	2.09	.40	0.5-4.0
Ara	6	1.6	0.95	.12	0.6-1.5	—	—	—	—	—
Str	2	0.5	0.80	.10	0.7, 0.9	—	—	—	—	—
Pso	1	0.3	1.80	—	—	—	—	—	—	—
Total	379	100.0	1.48	.19	0.4-4.3	185	100.0	1.73	.26	0.4-4.1

^a Arthropod orders are abbreviated as follows: Hym-F, formicid Hymenoptera; Hym-NF, non-formicid Hymenoptera; Dip-N, nematoceros Diptera; Dip-NN, non-nematoceros Diptera; Col, Coleoptera; Hem, Hemiptera; Thy, Thysanoptera; Hom, Homoptera; Ara, Araneida; Str, Strepsiptera; Pso, Psocoptera.

^b Comparison by Wilcoxon signed rank sum test of mean size of actual prey by order against overall mean size of actual prey with all orders combined. An asterisk identifies differences that are significant at the $P < .05$ level.

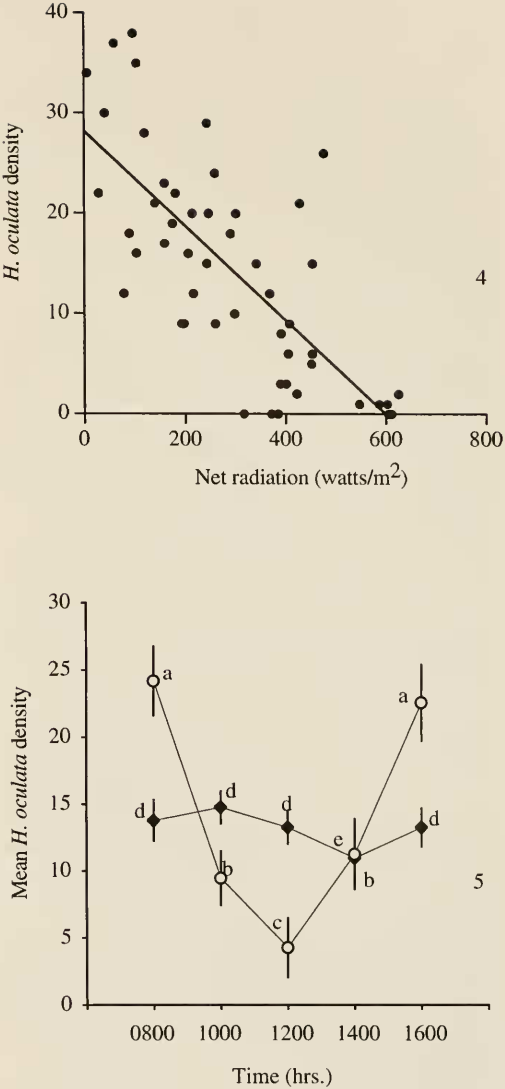
^c Comparison by Wilcoxon signed rank sum test of mean size of actual prey (days 8-10) by order against mean size of available prey (days 8-10) by order. An asterisk identifies differences that are significant at the $P < .05$ level.

^d Standard errors are presented in the table, but standard deviations (SD) were used in the statistical analyses.

smaller non-nematocerous Diptera prey than the average size available to it, and significantly larger Coleoptera. *H. oculata* chooses significantly larger formicid Hymenoptera than the overall average size of prey captured, and smaller non-formicid Hymenoptera and Araneida. This apparent size preference has also been observed in other robber flies (Hespenheide and Rubke 1977, Hespenheide 1978, Shelly 1984a)

The proportion of flies involved in the four activities (copulation, courtship, feeding, or other) at different times of the day is shown in Fig. 3. Copulation and courtship tend to peak in mid- to late afternoon and the proportion of flies feeding generally increases through the day. A linear regression shows a strong inverse relationship between fly densities and net radiation (Fig. 4; $P < .0001$; $r^2 = .54$) and a weaker inverse relationship between fly densities and ambient temperature ($P < .0001$; $r^2 = .34$), although these factors are correlated ($P < .0001$; $r^2 = .67$).

Differences in robber fly behavior between the shady and sunny transects further support the hypothesis that net radiation is the primary influence. The cycle of average daily robber fly density in the sunny and shady transects is shown in Fig. 5. During the study period, robber flies in the shady transect exhibited no significant change in average hourly density throughout the day whereas those in the sunny transect decreased significantly at midday compared to dawn or dusk. By 1400 h direct sunlight had entered the shady transect due to the sun's position at that hour, and the affect of this is represented in Fig. 5 as the period in the shady transect during which the fewest flies were counted. Flies in the shady transect tended to congregate in shady patches when sunlight entered the area, or relocate out of the transect. In the sunny transect, the few flies that chose to remain when net radiation was highest were found perched under grass blades, positioned in such a way so that the blade blocked the sun's rays. These observations indicate that the



Figs. 4–5. 4, Linear relationship between *H. oculata* density and net radiation: as net radiation increases fly density decreases ($P < .0001$; $r^2 = .54$). 5, The daily cycle of *H. oculata* in the sunny transect (open circles) and shady transect (closed circles). Data are shown as the mean density, $\pm$ SE, for each of five time periods for 10 separate days. Different letters represent significant differences among times within transects at $P < .05$ (Wilcoxon sign rank test); letters a–c refer to comparisons within the sunny transect, and letters d and e to comparisons within the shady transect.

flies may be responding primarily to incident radiation. Robber flies in general are believed to relocate to more shaded perches presumably to maintain a more “normal”

body temperature (Lavigne and Dennis 1975).

Fourteen pairs of *H. oculata* involved in courtship were observed in detail during this study with five resulting in the male joining the female in copulo. Males locate females by slowly cruising through the habitat close to the ground, pausing briefly to inspect perch sites for females. When a perched female is located, the male hovers several centimeters behind and slightly below the perched female and begins to fly upwards and make physical contact with her. Each time the male makes contact, the female's wings are pushed apart; possibly to provide him with an exposed abdomen to hold on to for leverage in initiating copulation. These collisions happen, on average, at about seven second intervals between which the male resumes the hovering position, rubbing his tarsae together prior to the next attempt. Once in copulo the pair remains attached, tail to tail with the female perched and the male dangling upside down, for an average of 11 minutes ($n = 5$). The female will often relocate to another perch, towing the male behind her. The nine unsuccessful courtship attempts ended with the female, apparently uninterested in courting the male, flying far enough away such that he lost track of her. The copulatory position I describe here for *H. oculata* is similar to that of *H. fusca* in North America (Dennis 1979).

Among the 80 *H. oculata* observed during the study of perch preference, most chose grasses (90%) over woody branch tips, herbs, and sedges in and around the study area, with a mean $\pm$ SE perch height of 45.5 ± 1.7 cm. The grass species and their order of perch preference included *P. conjugatum* (39%), *Digitaria* sp. (24%), *C. dactylon* (18%), and undetermined blades (19%). Among the major parts of an individual grass, 60% of robber flies preferred the tips of spikes, 28% the main part of the blade, 9% the tip of the blade, and 3% the stem of the spike. This clear preference for grasses, and for *P. conjugatum* in particular,

may be an artifact of their relative abundance being higher in these margins, which appears to be the case. Alternatively, *H. oculata* exhibits a species-specific perch behavior (see Fig. 1) like many asilids (Fisher and Hespenheide 1982, 1992), and grasses may present the optimal substrate for this.

Ectatomma ruidum seized the robber flies immediately in all 10 of the feeding trials. I conclude from this that, given the opportunity under non-experimental conditions, the ant would prey upon *H. oculata*.

Of 62 prey items removed from 18 orb-weaver webs, 47 were ant reproductives, nine were flies, and six were beetles. Interestingly, these orders also dominated the prey sampled from *Micrathena schreibersi* (Perty) webs in Panama (see Shelly 1984b). None of the orb-weaver's prey in my study were robber flies. The absence of robber flies as orb-weaver prey might be a result of robber flies cruising through the habitat at a slow enough rate as to evade becoming ensnared. I observed one case in which a robber fly collided with a web and immediately flew around it. Non-nematoceros Diptera are strong fliers and as a group have been found to be disproportionately represented in webs of *M. schreibersi* (Shelly 1984b), and this may likely be due to their ability to both avoid and escape becoming caught. This may explain the absence of *H. oculata* in orb-weaver webs during my study.

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